REVIEW

Impact of human disturbance on temporal partitioning within carnivore communities

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ABSTRACT

1. Interspecific competition is an important evolutionary force, influencing interactions between species and shaping the composition of biological communities. In mammalian carnivores, to reduce the risks of negative encounters between competitors, species can employ a strategy of temporal partitioning, adapting activity patterns to limit synchronous activity. This strategy of non-human competitor avoidance, however, may be influenced by the expansion of human activities, which has driven wild mammals towards nocturnality.

2. We hypothesise that the disruption of temporal niche partitioning by humans and their activities could increase temporal overlap between carnivores, enhancing interspecific competition.

3. We reviewed the published literature systematically and employed generalised linear models to evaluate quantitatively the relative influence of a range of human, meteorological and ecological variables on coefficients of temporal overlap within mammalian terrestrial carnivore communities (orders Carnivora and Didelphimorphia) on a global scale.

4. None of the models investigated showed evidence of an impact of humans on temporal partitioning between carnivores on a global scale. This illustrates that temporal avoidance of humans and competitors does not always follow a consistent pattern and that its strength may be context-dependent and relative to other dimensions of niche partitioning (spatial and trophic).

5. Similarly, the regulation of activity patterns may be strongly site-specific and may be influenced by a combination of biotic and abiotic characteristics. Temporal avoidance of both humans and competitors by carnivores may take the form of short, reactive responses that do not impact activity patterns in the longer term.

6. Although we did not detect a global disruption of temporal partitioning due to human disturbance, carnivore communities may still experience an increase in interspecific competition in other niche dimensions. Further research would benefit from using controlled experimental designs and investigating multiple dimensions of niche partitioning simultaneously. Finally, we recommend complementing the coefficient of temporal overlap with other metrics of fine-scale spatiotemporal interactions.

INTRODUCTION

Interspecific competition is an important component regulating biotic community structures (Schoener 1983, Wisheu 1998), and competing species must partition the resources they utilise to allow coexistence (MacArthur & Levins 1967). Resource partitioning is mostly achieved in three, often interacting, niche dimensions: the spatial, temporal, and trophic dimensions (Schoener 1974a). Many species can, for instance, adjust their activity patterns to reduce the risk of encountering dominant non-human competitors (Carothers & Jaksić 1984, Kronfeld-Schor & Dayan 2003). In most animal communities, temporal partitioning of activity may not be the primary strategy used to limit interspecific competition (Schoener 1974a). However, carnivores may use it more than any other taxa due to the severe risks of injuries associated with interference competition (Schoener 1974a, Palomares & Caro 1999, Hunter & Caro 2008). Indeed, temporal segregation of activity between carnivores has been observed on multiple occasions (e.g. Hayward & Slotow 2009, Bischof et al. 2014) and could be a strategy frequently used by subordinate carnivores to reduce negative encounters with dominant counterparts, fine-tuned by a reactive response to immediate risks (e.g. Broekhuis et al. 2013).

Humans, as apex predators (Darimont et al. 2015), produce predatory cues that are comparable to those of other natural competitors or predators (e.g. human voice; Frid & Dill 2002, Clinchy et al. 2016). Persecution by humans has driven behavioural adaptations in most mammalian species, including both predators and prey, to limit encounters with humans and reduce human-related mortality risks (Frid & Dill 2002, Ordiz et al. 2011), whilst being modulated by the intensity of persecution (Sazatornil et al. 2016). Such anti-predator behaviour in response to humans can be employed regardless of the underlying threat, and even non-lethal human disturbance can drive an avoidance response (Frid & Dill 2002). In this review, we use the idiom 'human disturbance' as a generic term that encompasses the immediate presence of humans (lethal and non-lethal) and any anthropogenic modification of the landscape.

As humans are mostly diurnal, carnivores can switch their activity patterns towards more nocturnal hours to avoid potentially negative interactions (Gaynor et al. 2018). Indeed, local increases in wild mammal nocturnality have been observed in direct response to variations in landscape-wide human-derived risks (e.g. during the hunting season; Di Bitetti et al. 2008, Stillfried et al. 2015; but see Theuerkauf 2009), reinforced by a lasting response to close human encounters (e.g. Ordiz et al. 2013, Clinchy et al. 2016). The intensity with which mammals adapt their circadian activity patterns to human disturbance may not be the same for all species, and depends on their behavioural plasticity and life-history characteristics (Lendrum et al. 2017). However, a recent meta-analysis by Gaynor et al. (2018) suggests that the pattern of increased nocturnality is observed globally and could be a common response from wild mammals facing human disturbance. In undisturbed areas, carnivores need to operate a trade-off between obtaining optimal resources and avoiding dominant competitors (Hayward & Slotow 2009). In human-altered habitats, carnivores may need to incorporate a third crucial element to this trade-off by avoiding humans. Therefore, since temporal partitioning is a common strategy used by carnivore species to coexist, and humans can impact on the activity patterns of species, human disturbance could interfere with the strategy of temporal partitioning between competing carnivores.

Disruption of niche partitioning can increase interspecific competition and may have multiple ecological and community consequences (Sévêque et al. 2020). However, niche partitioning is a multidimensional dynamic process, and an increase in overlap in one niche dimension may be compensated by a decrease in another (Schoener 1974a). Therefore, interspecific competition may not necessarily be a direct result of the niche overlap in a single dimension. Similarly, not all carnivore species may be impacted equally by human disturbance, and the intensity of the avoidance response to humans may vary among species (e.g. Caruso et al. 2016). Due to direct threat, competition with humans for food and depredation on livestock, apex carnivores typically experience most persecution (Inskip & Zimmermann 2009) and live in a landscape of fear of human-related mortality (Oriol-Cotterill et al. 2015). As a consequence, large carnivores have indeed been observed to shift their activity towards nocturnal hours (Gaynor et al. 2018). However, mesocarnivore species that are more tolerant of human disturbance (e.g. Gosselink et al. 2003) may shift their activity pattern to a lesser degree when facing human disturbance, thus maintaining temporal partitioning with dominant apex predators (Frey et al. 2020). Unequal sensitivity to humans can induce a behavioural mesopredator release, wherein disturbance-induced alterations of activity pattern in large carnivores benefit the fitness of mesocarnivores by increasing the amount of time allocated to other activities (e.g. foraging; Brown et al. 1999). In addition, apex predators are typically found in lower densities in areas under higher human disturbance (Wolf & Ripple 2017), which may then limit the need for medium-sized carnivores to alter their activity pattern in response to the risk of encountering dominant competitors in disturbed landscapes.

Many carnivores now live in environments that are under human pressure, and are subject to a combination of bottom-up (e.g. modification of the landscape; Chapron

et al. 2014, Venter et al. 2016) and top-down (e.g. hunting; Darimont et al. 2015, Ripple et al. 2016) anthropogenic forces. The impact of human disturbance on a wide range of biological interactions has been widely studied (e.g. intraspecific competition; Nevin & Gilbert 2005, predator–prey interactions; Muhly et al. 2011, animal–plant interactions; Neuschulz et al. 2016). Moreover, we know that human disturbance has already reduced the niche available to animals in other dimensions (e.g. trophic, Creel et al. 2018, spatial, Tucker et al. 2018), which can result in large-scale increases in niche overlap (Manlick & Pauli 2020). However, our knowledge of the influence of humans on coexistence and temporal niche partitioning between carnivores is still limited. Thus, there is a need to address this question, since not only can temporal displacements and reductions in activity carry costs that reduce species fitness (e.g. Beale & Monaghan 2004, Ciuti et al. 2012), they can also alter the way species interact, which can have cascading implications (Suraci et al. 2019).

To address this knowledge gap, we conducted a global systematic and quantitative review of the temporal niche partitioning between mammalian terrestrial carnivores (orders Carnivora, Didelphimorphia). Based on *a priori* knowledge of the factors influencing wild mammals' activity patterns, we investigated diverse human, meteorological and ecological factors as potential determinants of temporal partitioning within carnivore communities. Drawing on a global data set covering a variety of ecosystems, carnivore communities and types of human disturbance, this study had two objectives: 1) to investigate whether human disturbance affects temporal niche partitioning uniformly and on a global scale; 2) to test the effect of additional meteorological and ecological factors that are hypothesised to influence niche partitioning, either on their own or through interactions with human disturbance.

METHODS

Literature search

To investigate temporal niche partitioning between carnivores, we performed a literature search in December 2019 and examined all articles and grey literature citing the coefficient of temporal overlap method proposed by Ridout and Linkie (2009). This method knows a growing popularity in the science of animal behaviour, illustrated by a rapidly increasing rate of citation (Fig. 1). Hence, it has been widely accepted as one of the preferred methods to investigate temporal partitioning between animals, using camera trap data (i.e. time-stamped images of species in a known location). The coefficient of overlap uses a kernel density estimation method that ranges from 0 (no overlap) to 1 (complete overlap). Additionally, 95%
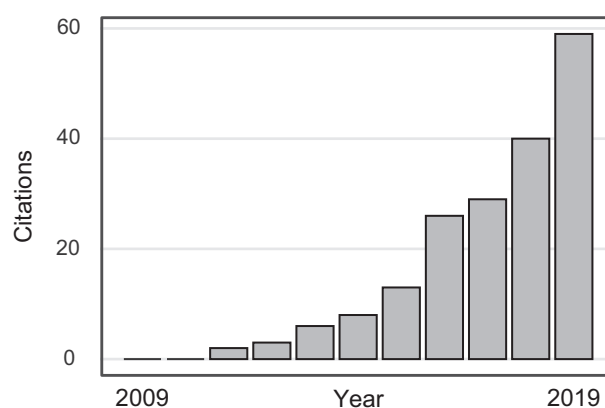

Fig. 1. Number of citations per year from 2009 to 2019 for the article by Ridout and Linkie (2009), based on the Springer citation tool (https://citations.springernature.com). In this article, the coefficient of temporal overlap method used in all papers included in our analysis is proposed.

confidence intervals can be calculated via bootstrap sampling (Ridout & Linkie 2009).

We extracted all articles citing Ridout and Linkie's (2009) method from Scopus (where it was cited 212 times; www.scopus.com), Web of Science (cited 195 times; www.webofknowledge.com) and Google Scholar (cited 338 times; https://scholar.google.com). After removing duplicates, we assessed 356 articles for eligibility. We restricted records to studies in which the coefficient of temporal overlap was calculated for at least one pair of sympatric mammalian terrestrial carnivore species (belonging to the order Carnivora, Didelphimorphia or Dasyuromorphia). In addition, we removed studies in which one of the carnivores was an invasive species, because the recent sympatry of invasive species may not have allowed sufficient time for native species to develop a consistent strategy of temporal avoidance (e.g. Fancourt et al. 2019). Finally, we discarded species combinations, which were present only once in the data set. By doing this, we focused the analysis on variations in temporal overlap within species combinations facing different anthropogenic and environmental conditions. Therefore, each species combination included in the analysis had at least two coefficients of temporal overlap, extracted from at least two different study areas. In the end, we included 42 studies in the quantitative analysis and final synthesis (Appendix S1).

Data extraction

We extracted the coefficients of temporal overlap between pairs of carnivore species from the results sections of the 42 studies. For every value of temporal overlap, we recorded the following information on the interacting carnivore species: species name; taxonomic family; average adult body mass; and baseline activity pattern (Table 1).

Table 1. Description, spatial resolution, range of variability and source of the variables extracted for each study area and included in the *a priori* models of temporal resource partitioning by 217 pairs of carnivore species

Variable	Description	Scale	Mean ± SD (range)	Source
Human density	Average inhabitants / km^2 in the study area during the year of data collection. For studies that span over more than one year, the first year was selected.	1 km	84.5 ± 181.1 (0.1–886)	WorldPop (Lloyd et al. 2017)
Built-up environment	Percentage cover (%) of built-up environment in the study area in 2015.	100 m	2.9 ± 5.8 (0–27.3)	Copernicus 2015 global land cover database (Buchhorn et al. 2019)
Pasture	Percentage cover (%) of pastures in the study area in 2000.	10 km	20.8 ± 22 (0–91.1)	Global Agricultural Lands: Pastures, 2000 (Ramankutty et al. 2008)
Simpson's landscape diversity index	Simpson's landscape diversity index (SIDI) in the study area calculated from a discrete land cover classification in 2015. Land cover classes comprised shrubs, herbaceous vegetation, crops, built-up, bare, wetland, closed forest and open forest.	100 m	0.3 ± 0.3 (0–0.7)	Copernicus 2015 global land cover database (Buchhorn et al. 2019); Fragstats v4 for calculating SIDI (McGarigal et al. 2012)
Precipitation	Annual precipitation (mm) in the study area, averaged for the 1970-2000 period.	1 km	1148.1 ± 800.8 (215–3149.9)	WorldClim (Fick & Hijmans 2017)
Temperature	Annual mean temperature (°C) in the study area, averaged for the 1970-2000 period.	1 km	18.2 ± 6.4 (0.6–28.4)	WorldClim (Fick & Hijmans 2017)
Carnivore community richness	Number of mesocarnivores (MC) and large carnivores (LC) inhabiting part or all of the study area, using the 2019 International Union for Conservation of Nature (IUCN) Red List update.	n/a	MC: 12.9 ± 5.5 (5–27) LC: 1.3 ± 2.0 (0–8)	IUCN Red List of Threatened Species (IUCN 2020)
Body mass ratio	Average body mass of larger species / Average body mass of smaller species.	n/a	7.4 ± 11.1 (1–73.8)	PanTHERIA database (Jones et al. 2009)
Baseline activity pattern	Species activity pattern: (1) nocturnal, (2) cathemeral or crepuscular, (3) diurnal.	n/a	(1): 18. (2): 24. (3): 1	PanTHERIA database (Jones et al. 2009)

To investigate the effect of anthropogenic and environmental conditions on coefficients of temporal overlap, we extracted the approximate geographic centre and size of every study area from the methodology section, when clearly stated, or through visual estimation of the maps provided in the articles. Based on *a priori* knowledge of factors affecting circadian activity patterns of carnivores, we then averaged the following characteristics of the landscape within each study area: human density; percentage of built-up environment; percentage of pasture; Simpson's landscape diversity index; annual precipitation; and annual mean temperature and carnivore community richness (see Table 1 for detailed methodology, source, spatial resolution and description of each variable). To ensure maximum consistency in the landscape metrics between study areas, we used solely global databases. We therefore operated a trade-off between spatial resolution (which could have been finer if we had used appropriate local databases for each study area) and homogeneity in the methods of calculation for each variable. We did not aim to measure fine-scale temporal responses of animals to each of the

variables of interest, but rather to detect a global response to human disturbance. Therefore, we did not incorporate the variability in landscape characteristics within each study area in the analysis, but instead focused on variability between sites. When studies indiscriminately grouped their camera-trap data from more than one location, we averaged the value of each study area to create a unique value that best represented the overall conditions of the surrounding landscape. Spatial analysis was performed using a Geographical Information System (ArcGIS v10.7.1; ESRI, Redlands, California, USA).

Paired studies

First, we qualitatively evaluated the findings of all studies in which the causal effect of human disturbance on temporal partitioning between carnivores (i.e. increase, decrease or no effect) was investigated by using an experimental or quasi-experimental design (i.e. studies with a simultaneous experimental control; Hone 2007). Typically, such studies calculated and compared the coefficients of temporal

overlap of similar species combinations between areas classified as having low and high levels of human disturbance. We were interested in the type of human disturbance that was investigated and in whether the authors were able to demonstrate a clear change in the coefficients of temporal overlap between the areas under low or high human disturbance (i.e. when the 95% confidence intervals of the two coefficients did not overlap).

Global models

Using knowledge from published studies of factors affecting circadian activity pattern of carnivores, we explored ten hypotheses, as models covering human, meteorological and ecological factors that could affect the coefficient of temporal overlap between carnivore species (Table 2; see 'Global model justification' below). Thus, we considered the coefficient of temporal overlap as the dependent variable, and models were fitted using generalised linear mixed models (Zuur et al. 2009), with a logit link function and beta distribution, appropriate for continuous variables restricted to an interval between 0 and 1 (Ferrari & Cribari-Neto 2004). We added species combination as a random effect in each model, with levels representing different locations where the species combinations were studied, and conducted model selection using the Akaike information criterion (AIC; Akaike 1981). Having a minimum of two replicates per species combination, and adding it as a random factor, allowed us to artificially create a paired comparison design (Montgomery 2017). By doing so, we could focus on the variance in coefficients of overlap explained by the different explanatory variables within species combinations, rather than testing the variance between species combinations. The coefficient of temporal overlap is a derived measure based on modelled activity patterns and is associated with uncertainty (commonly provided as 95% confidence intervals). However, we chose not to account for the variance associated with the dependent variable in the analysis, because numerous studies included in this review did not provide the uncertainty associated with their coefficients of temporal overlap, nor the number of detections used to model activity patterns (which is inversely proportional to the width of the confidence intervals). Discarding these studies would have significantly reduced the number of studies included in our global analysis, and we elected to favour a larger sample size over more sophisticated models. Nonetheless, coefficients of temporal overlap computed from the activity pattern of species detected fewer than 10 times were not included in this analysis, since their accuracy and precision cannot be guaranteed (Lashley et al. 2018).

When no single model is clearly superior to the others in the set (e.g. typically $AIC_w \geq 0.90$), extracting information from single models can lead to weak inferences, and multimodel inference should be favoured (Burnham & Anderson 2002). As this occurred in our case (see 'Results'), we applied a model-averaging technique to the top-ranked models with similar AIC ($\Delta AIC < 2$), to build a full average model with 95% confidence. We calculated Spearman's rank correlation coefficients (ρ) to investigate multicollinearity between the continuous predictors and prevented highly correlated variables ($\rho > 0.70$, Zar 2010) from being included in the average model. All modelling analyses were performed using the R packages 'glmmADMB' (Skaug et al. 2016) and 'MuMln' (Kamil 2019) in R version 3.6.1 (R Core Team 2018).

Global model justification

Carnivores have been found to increase their nocturnal activity in habitats under higher human disturbance (e.g. urban areas; Carter et al. 2015, Lewis et al. 2015, Wang et al. 2015), which can lead to higher temporal overlap among carnivore species (Table 2; Hypotheses 1 and 2). Such temporal avoidance of humans may be especially predominant in pastoral landscapes, where human-related mortality risks are higher due to human–carnivore conflicts emerging from livestock depredations (Frank & Woodroffe 2001), therefore potentially increasing temporal overlap between carnivores even further in pastoral landscapes (Table 2; Hypothesis 3). Conversely, landscapes that are kept under traditional mosaic management, with a mix of natural and anthropogenic land use, can facilitate habitat selection and temporal partitioning (Monterroso et al. 2014, Curveira-Santos et al. 2017) and could reduce temporal overlap between species (Table 2; Hypothesis 4). Nevertheless, the reduction of temporal overlap attributed to higher landscape diversity may be diminished in landscapes with a higher proportion of areas associated with extensive grazing systems (Table 2; Hypothesis 5).

The daily activity patterns of animals can also be regulated by meteorological and ecological factors, which could influence the way carnivore species interact with each other. For instance, in arid landscapes, where water features are a scarce and spatially fixed resource, there is little opportunity to achieve spatial avoidance of dominant competitors (Atwood et al. 2011). Thus, subordinate species can concentrate their activity at times where their dominant counterparts are less active (Atwood et al. 2011, Edwards et al. 2017), potentially reducing temporal overlap (Table 2; Hypothesis 6). In habitats with high daytime temperatures, shifting activity to night-time may help species reduce thermal stress (Fuller et al. 2016, Rabaiotti & Woodroffe 2019). However, this could reduce the temporal niche available to segregate from competitors (Astete et al. 2017), thus increasing temporal overlap (Table 2;

Table 2. *A priori* models testing 10 hypotheses in which human, meteorological and ecological continuous variables are predictors of coefficients of temporal overlap between sympatric carnivores. Hypothesis justification and support can be found in the text; * indicates interaction

Hypothesis tested	Variables in the model	Impact on temporal overlap
1. Humans' diurnal activity is associated with increased nocturnality in carnivores.	Human density	Increase
2. Human disturbance is higher in urban areas, which leads to carnivores in urban areas being more nocturnal than those in rural areas.	Built-up environment	Increase
3. Livestock depredation is a source of human-carnivore conflict. Frequent lethal management of carnivores in pastoral landscapes is associated with increased carnivore nocturnality.	Pasture	Increase
4. Complex habitat mosaics nurture rich communities, and temporal partitioning is selected to facilitate stable coexistence.	Simpson's landscape diversity index	Decrease
5. The effects of landscape diversity are diminished in landscapes with a higher proportion of pastures.	Simpson's landscape diversity index * pasture	Non-linear
6. Scarcity of spatially fixed water sources in dry areas forces temporal partitioning.	Precipitation	Increase
7. Extremely high temperatures drive crepuscular or nocturnal behaviour.	Temperature	Increase
8. The effects of precipitation are magnified in extremely hot areas.	Precipitation * temperature	Non-linear
9. In richer communities, temporal partitioning is selected to facilitate stable coexistence.	Carnivore community species richness	Decrease
10. Species combinations with higher body mass ratios invest less in temporal partitioning, and more in spatial partitioning, to improve coexistence.	Body mass ratio	Increase

Hypothesis 7). In addition, cases of extreme thermal stress may cause most or all species to shift to nocturnal activities, rendering temporal partitioning at water sources unachievable. Therefore, any increase in temporal overlap through increased precipitation would be negated by higher daytime temperatures (Table 2; Hypothesis 8).

The strength and outcomes of species interactions are also dependent on the community composition and the interacting species (Sentis et al. 2017). In species rich, and thus more complex, carnivore communities, temporal partitioning may facilitate stable coexistence between co-occurring species (Monterroso et al. 2014). Therefore, higher carnivore species richness could decrease the average temporal overlap within the community (Table 2; Hypothesis 9). Alternatively, temporal overlap among some pairs of species could increase in areas with higher species richness, given that there are more species to avoid, leading to trade-offs and thus higher overlap with some species in the community (Curveira-Santos et al. 2017). Additionally, carnivore species with similar body mass have higher potential for competition, especially if they have similar diets (Wilson 1975). Smaller carnivores may also be at more risk of intraguild predation from larger carnivores (Woodward & Hildrew 2002). Edwards et al. (2015) observed that species combinations with bigger differences in body mass (higher body mass ratios) used spatial partitioning to a greater extent than temporal partitioning. Conversely, species combinations with lower body mass ratios may invest in temporal partitioning to facilitate stable coexistence (Di Bitetti et al. 2010, Edwards et al. 2015). Therefore, temporal overlap may increase with high body mass ratios (Table 2; Hypothesis 10).

RESULTS

Description of the literature

Altogether, we extracted 217 coefficients of temporal overlap from 42 studies (Fig. 2). The coefficients of overlap ranged from 0.12 to 0.95 (mean ± standard deviation, SD = 0.68 ± 0.16), with a seemingly similar distribution between continents (Fig. 3). There was a high disparity between continents, with most coefficients extracted from studies in North America (102 values from 9 studies), followed by Europe (55 values from 7 studies), Asia (42 values from 16 studies), South America (13 values from 6 studies) and, finally, Africa (5 values from 4 studies). Except for human density and built-up environment ($\rho = 0.78$), the predictors extracted (Table 1) were not highly correlated with one another.

A total of 74 species combinations were investigated (Appendix S1); the mean coefficient of temporal overlap was 2.93 (SD: 1.93, range 2–12). Almost half of the studies ($n = 20$) investigated a single species pair, whilst the other studies ($n = 22$) investigated 2 to 20 species pairs simultaneously (mean = 5.41 ± 4.75 SD). This review included a total of 43 species, of which 41 belong to the order Carnivora, two to the order Didelphimorphia, and none to the order Dasyuromorphia. From all species, 18 were strictly nocturnal, 24 were crepuscular or cathemeral, and only one species, the yellow-throated marten *Martes flavigula,* was strictly diurnal. Felidae was the most investigated family ($n = 140$), followed by Mustelidae ($n = 114$), Mephitidae ($n = 60$), Canidae ($n = 50$), Procyonidae
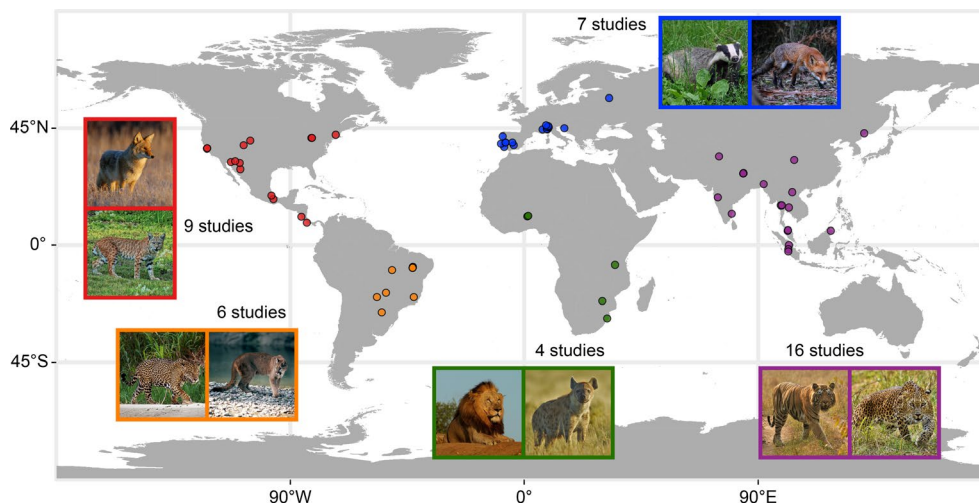
Fig. 2. Geographical locations of the study areas included in this review, colour-coded by continent. In several cases, research was conducted in more than one study area. Photos show the carnivore species pair that was the most studied in each continent, as follows: North America: coyote *Canis latrans* and bobcat *Lynx rufus*, South America: jaguar *Panthera onca* and mountain lion *Puma concolor,* Africa: African lion *Panthera leo* and spotted hyena *Crocuta crocuta*, Asia: tiger *Panthera tigris* and leopard *Panthera pardus*, Europe: European badger *Meles meles* and red fox *Vulpes vulpes*. Photo credits can be found in Appendix S3; map design adapted from Prugh and Sivy (2020).

($n = 34$), Viverridae ($n = 14$), Didelphidae ($n = 10$), Herpestidae ($n = 6$) and Hyaenidae ($n = 6$).

Paired studies

Eight studies investigated the effects of human disturbance by comparing the coefficients of temporal overlap of species pairs between areas classified as having low or high human disturbance (Appendix S2). Of these, two studies were able to demonstrate clearly that some temporal overlap between carnivores were increased in areas with high human disturbance (i.e. the confidence intervals between low- and high-disturbance areas did not overlap; Lewis et al. 2015, Wang et al. 2015), one study reported significantly lower temporal overlap in areas with high human disturbance (Baker 2016), and five found no apparent difference (i.e. comparison of coefficients without confidence intervals; Cruz et al. 2015) or no significant change attributed to human disturbance (i.e. the confidence intervals between sites with low and high disturbance overlapped; Carter et al. 2015, Rayan & Linkie 2016, Moll et al. 2018, Sogbohossou et al. 2018). The three studies that attributed either increases or decreases in temporal overlap to human disturbance in some species pairs also reported no change in other species pairs.

Global models

None of the models explored had strong support (Table 3). The evidence ratios (i.e. AIC_{w1}/AIC_{w2}) for the best model (interaction between Simpson's landscape diversity index

and pasture) versus the second (built-up environment) and third best (Simpson's landscape diversity index) best models were low (2.15 and 3.07, respectively), making the model selection uncertainty high. Therefore, we applied a model-averaging technique to the two top-ranked models with similar AIC ($\Delta AIC < 2$; interaction between Simpson's landscape diversity index and pasture, and built-up environment), to build the full average model with 95% confidence.

None of the variables included in the full average model was a significant predictor of coefficients of temporal overlap between carnivores (Table 4). The standard errors of the estimate for built-up environment and the interaction between Simpson's landscape diversity index and pasture overlapped with zero, further indicating weak relationships. Simpson's landscape diversity index and built-up environment were positively associated with temporal overlap, whilst pasture showed a negative relationship with temporal overlap (Table 4, Fig. 4). The lack of statistical significance and weak relationships found suggests that no human, environmental or meteorological variables are global predictors of carnivore temporal overlap.

DISCUSSION

Although accumulating evidence suggests that human disturbance increases nocturnal activity in wild mammals (Gaynor et al. 2018, Nix et al. 2018), we found no evidence at a global scale for an impact of the selected human, environmental or meteorological variables on temporal partitioning between carnivores.
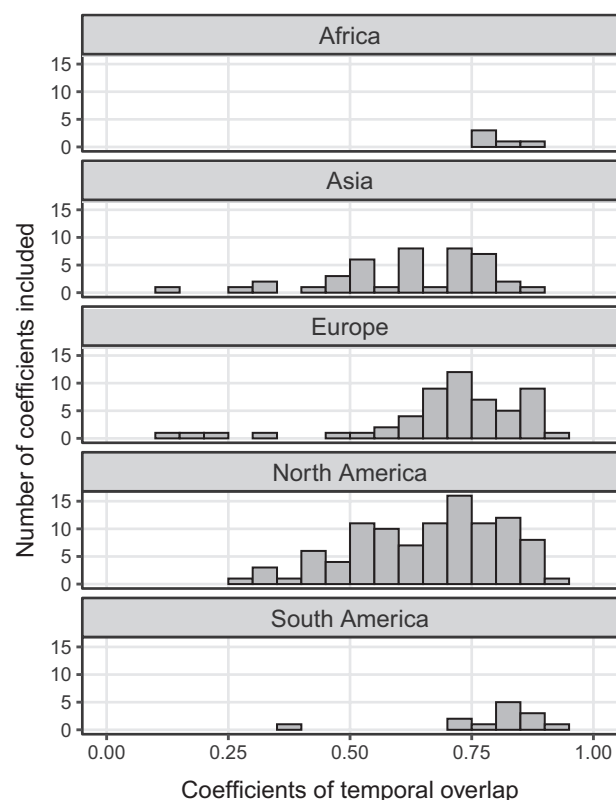
Fig. 3. Distribution of the coefficients of temporal overlap between pairs of carnivore species, extracted from the literature for this review, grouped by continent.

Whilst the statistical models do not provide evidence for a global effect of human disturbance on temporal partitioning between carnivores, it cannot be said that human disturbance has no impact on temporal partitioning. Rather, the effects of human disturbance are diverse and probably context-dependent, as illustrated by findings from the eight studies that compared temporal overlap in low and high human disturbance treatments. As hypothesised (Hypothesis 2), in two of these studies, some species, but not all, increased nocturnal activity in response to higher urbanisation, which increased temporal overlap between competitors (Lewis et al. 2015, Wang et al. 2015). Conversely, Baker (2016) documented that, although human disturbance – quantified as a combination of paved roads and hiking trails – induced an increase in wild mammal nocturnality, most temporal overlaps between species were lower in more disturbed areas than in less disturbed areas. This is because species within disturbed landscapes may co-occur in safe areas to a greater extent, and subordinate species can fine-tune their temporal partitioning with dominant competitors by narrowing or displacing their peaks of activity. Indeed, maintaining temporal partitioning with competitors in a reduced,

nocturnal, temporal window can be a strategy adopted to ensure avoidance of both humans and competitors simultaneously (e.g. Sogbohossou et al. 2018). Such fine-scale adaptations may not be detected by diel measurements of temporal overlap, which could be one of the reasons for the lack of a significant trend in these results. Similarly, it is possible that, despite an increased nocturnality caused by human disturbance, carnivores adjust their activity patterns on a fine temporal scale to avoid both humans and competitors simultaneously, therefore not increasing the temporal overlap among carnivores. This could explain why the remaining five studies reported relatively similar coefficients of temporal overlap in areas under low and high human disturbance (e.g. human activity: Carter et al. 2015, Sogbohossou et al. 2018; plantations and reduction in landscape diversity: Cruz et al. 2015, Rayan & Linkie 2016; built-up environment: Moll et al. 2018). In addition, the lower density of large carnivore populations in high human density areas (Woodroffe 2000), coupled with a high anthropogenic resource availability, could relax competition among carnivores able to adapt to human disturbance (Ruscoe et al. 2011, Wolf & Ripple 2017), thus reducing the importance of temporal partitioning in promoting stable species coexistence. Another explanation could be that the baseline activity pattern of species included in the analysis (i.e. diurnal, nocturnal or crepuscular/cathemeral) may influence the findings. An effect of human disturbance on overlap may be less likely between nocturnal–nocturnal pairs, but could be expected in diurnal–crepuscular pairs. However, the strong dearth of diurnal species in the studies included in the analysis

Table 3. Results of the *a priori* model selection for predictors of coefficients of temporal overlap between sympatric carnivores, with models ranked based on their AIC. The number in parentheses indicates the hypothesis tested by each model (Table 2). Species combination was added as a random factor in each model; * indicates interaction. Models in bold were selected to build the full model average

Model (hypothesis tested)	AIC	ΔAIC	AIC_w
Simpson's landscape diversity index * pasture (5)	**−258.82**	**0.00**	**0.43**
Built-up environment (2)	**−257.32**	**1.50**	**0.20**
Simpson's landscape diversity index (4)	−256.53	2.29	0.14
Pasture (3)	−255.68	3.14	0.09
Precipitation * temperature (8)	−253.96	4.86	0.04
Temperature (7)	−253.78	5.04	0.03
Null (intercept only)	−253.39	5.43	0.03
Precipitation (6)	−251.97	6.85	0.01
Body mass ratio (10)	−251.42	7.40	0.01
Human density (1)	−251.41	7.41	0.01
Carnivore community species richness (9)	−250.96	7.86	0.01

Table 4. Full model average of the two best *a priori* models (ΔAIC < 2), with 95% confidence. Species combination was added as a random factor. All explanatory variables were standardised for comparison purposes. SE, Standard Error; * indicates interaction

Variable	Estimate	SE	*z* value	*P*-value
(Intercept)	0.699	0.077	9.077	<0.005
Pasture	−0.056	0.053	1.054	0.292
Simpson's landscape diversity index	0.068	0.055	1.229	0.219
Built-up environment	0.047	0.053	0.888	0.375
Simpson's landscape diversity index * pasture	0.025	0.043	0.588	0.557

created a severe unbalance between groups and low sample size for species pairs with a diurnal carnivore, so we could not include the baseline activity patterns of species in our analysis. Similarly, we did not account for the uncertainty associated with the coefficient of temporal overlap, and identical weight was given to all the coefficients included in our analysis. However, the precision and accuracy of the coefficient of temporal overlap increases with the number of species detections used to model activity patterns (Lashley et al. 2018). This shortcoming may have reduced the precision of our analysis, but we do not believe that it changed the overall results and conclusions presented in this review.

None of the ecological or meteorological factors was a significant predictor of coefficients of temporal overlap. Temporal overlap was hypothesised to decrease with higher landscape diversity (Hypothesis 4), as complex habitats enable fine-scale habitat segregation and promote species richness (Rosenzweig 1981, Pereira et al. 2012). However, temporal overlap increased with the Simpson's landscape diversity index, contrary to Hypothesis 4, but the relationship was weak. Although previous studies observe that temporal segregation is indeed likely to play a role in complex communities (Monterroso et al. 2014), it is possible that, in the data set used in this study, higher landscape diversity did not increase species richness systematically, due to other external factors (e.g. habitat

fragmentation; Rybicki et al. 2020). Another possibility is that species richness did indeed increase with landscape complexity, but that temporal partitioning was not selected as a primary mechanism allowing coexistence with competitors. In the latter case, species-specific temporal preferences may reflect strategies unrelated to competitive interactions (e.g. foraging strategies; Curveira-Santos et al. 2017). Carnivore community richness (Hypothesis 9), body mass ratio (Hypothesis 10), temperature (Hypothesis 7) and precipitation (Hypothesis 6) were not included in the average model.

Internally, the circadian rhythm is governed by each species' biological clock, an endogenous programme that dictates the timing of many behaviours (Pittendrigh 1981). Externally, this is regulated by biotic factors (e.g. competitor avoidance; predators matching their activity to that of their prey; Gantchoff & Belant 2016) and abiotic factors (e.g. daytime temperature; Rabaiotti & Woodroffe 2019). As competitor avoidance is just one the many factors regulating activity pattern, it may not be selected in systems where other factors are more limiting to the species' fitness (Schoener 1974b). This is seen, for example, in systems with harsh environmental conditions or low prey availability (Cozzi et al. 2012, Broekhuis et al. 2014, Astete et al. 2017). In other systems, where none of the governing factors exerts an extreme pressure on the individuals' fitness, activity pattern can be governed by a combination
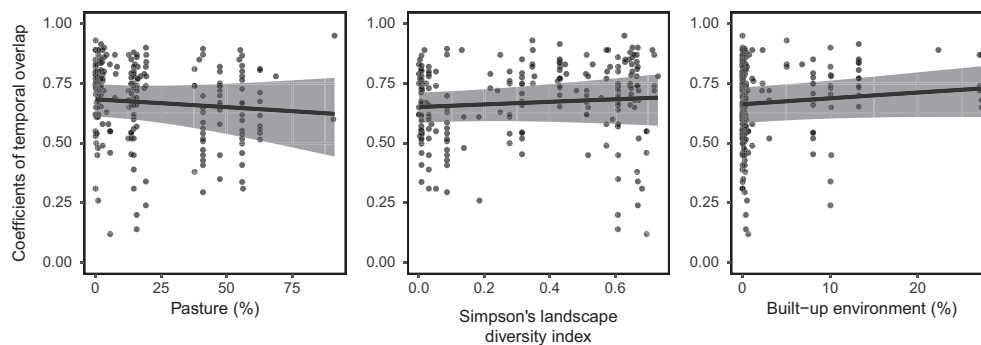

Fig. 4. Predicted effects of the explanatory variables included in the full model average on coefficients of temporal overlap. The grey ribbon represents the 95% confidence intervals.

of several interacting factors (e.g. moonlight and prey activity; Penteriani et al. 2013). Thus, the relative strength of each external factor regulating circadian activity patterns may be strongly related to the biotic and abiotic conditions of the surrounding landscape. This site specificity renders the investigation of temporal partitioning on a global scale ineffective, by yielding incomplete results that cannot be applied locally.

Limitations

There are two main limitations to this study that could explain the weak relationships found between the predictors investigated and coefficients of temporal overlap. First, the data we collected may be too coarse to analyse processes happening at much smaller spatial and temporal scales. Concerns over spatial scaling and perception bias in ecology have been raised before (Wiens 1989, Levin 1992). As characteristics of the landscape change with spatial scale (Turner et al. 1989), it is possible that some environmental variables have an influence on activity pattern and temporal partitioning among carnivores, albeit on a different spatial grain than what was used in this analysis. For the purpose of this study, we decided to prioritise the use of standardised variables, by using the same large-scale indices for all studies. Although doing so meant using a coarser spatial grain, with reduced precision, it ensured complete comparability between study sites. For instance, several studies measured levels of human activity as the average number of photographs of people at camera-trap sites (e.g. Wang et al. 2015, Moll et al. 2018). Such a fine-scale spatiotemporal metric cannot be determined *a posteriori*, and we were therefore unable to apply it to all studies in this review. To address this issue, future surveys should favour well-designed, purpose-driven data collection that record the characteristics of the surrounding landscape systematically whilst deploying cameras in the field, enabling the investigation of ecological processes on different spatial scales simultaneously (e.g. Wilmers et al. 2013). This recommendation may be particularly relevant for variables describing the immediate presence of humans. In this study, we used human density as a proxy for the probability of encountering humans, but this relationship may not always hold true (e.g. some natural parks may experience peaks in numbers of human visitors on a regular basis, but have a low recorded human density due to the lack of habitations). Although measuring human activity on camera can prove ethically challenging (Brittain et al. 2020, Sharma et al. 2020), we believe it is needed to comprehend the fine-scale temporal responses of wild animals to the immediate presence of humans.

Second, the coefficient of temporal overlap, which is based on the daily activity patterns of species, may not be the best-fitting tool to investigate temporal partitioning. Daily activity patterns are typically calculated by indiscriminately grouping data spanning several days, months or years into a 24-hour window. Evaluating temporal partitioning in such a way assumes that competitor avoidance is a predictive process, with long-lasting and consistent effects. Instead, competitor avoidance may often be a reactive response, in which subordinate species adapt their use of landscape to the nearby presence of competitors in temporal scales that are too small to have lasting effects on the circadian activity pattern (Broekhuis et al. 2013, López-Bao et al. 2016). Likewise, although humans' influence on wild mammals' behaviour may exceed that of natural predators (Ciuti et al. 2012, Clinchy et al. 2016), it is likely that the broad-scale nocturnal adaptations of carnivores to humans and human features work in combination with finer-scale immediate responses to human stimuli (e.g. Ordiz et al. 2013, Moll et al. 2018). Alone, the coefficient of temporal overlap portrays a broad picture of temporal segregation and is best paired with an ecological interpretation of the activity curves (where the peaks are, how narrow, etc.), or with other metrics of fine-scale temporal interactions, such as time-to-event analysis (e.g. Prat-Guitart et al. 2020). Similarly, combining metrics of temporal association with spatial displacement metrics (e.g. multispecies occupancy models; Mackenzie et al. 2004, Rota et al. 2016) or spatiotemporal models (e.g. co-detection modelling: Cusack et al. 2017; time-dependent observation modelling: Ait Kaci Azzou et al. 2021) can yield a more complete picture of fine-scale avoidance of competitors, and how human disturbance might be mediating these interactions. The coefficient of temporal overlap is a useful tool in measuring the average temporal overlap between species and large-scale responses to human disturbance, but it can overlook fine-scale interactions that are essential to allow coexistence. In addition, studies that indiscriminately group data over long periods of time may overlook seasonal variations in behaviour (e.g. Monterroso et al. 2014, Caravaggi et al. 2018), especially if they do not account for the variation in daylength throughout the year in their analysis (i.e. by using solar time instead of clock time; Nouvellet et al. 2012, Vazquez et al. 2019). These studies are thus at risk of recording faulty behavioural timings, which can lead to erroneous conclusions on the way species share time. Similarly, camera-trap surveys focusing on calculating activity patterns and temporal partitioning do so by grouping the data from the different stations within their study area. However, consequential variations in human disturbance or habitat features across individual camera stations could impact species' behaviour on a fine scale. Finally, the coefficient of temporal overlap is a pairwise approach to evaluating temporal partitioning. Interspecific

competition and niche partitioning are complex systems, with many species involved. Restricting the investigation of temporal partitioning to two species, without considering the impact of the presence and activity of other species forming the community, essentially distils complex patterns of multispecies partitioning into dyads. For all the reasons detailed above, it is in the best interest of studies that employ camera traps to avoid overinterpreting coefficients of temporal overlap to investigate the potential for competition among sympatric species.

CONCLUSIONS

Undoubtedly, humans affect the activity patterns of wild mammals, but we found no evidence that this process could impact temporal overlap between carnivores consistently on a global scale. Instead, the influence of humans on temporal partitioning may be diverse and context-specific and thus requires further investigation due to the theoretical implications for community structure. Similarly, we found no strong evidence that the ecological and meteorological factors investigated were significant predictors of temporal partitioning between carnivores globally. Therefore, temporal avoidance of competitors may be regulated by multiple factors simultaneously, and the relative strength of each factor may vary with the biotic and abiotic conditions of the landscape.

Large-scale analyses such as this one can yield valuable and statistically powerful results. Conducting such investigations on a global scale allows the inclusion of a large range of human activities and landscape transformations, providing valuable insights into the role of humans on species coexistence in animal communities. However, large-scale analyses can also mask local variability in the response of the processes investigated. Our investigation of human disturbance on temporal partitioning among carnivores suffered a lack of controlled studies, a common issue in carnivore science (Allen et al. 2017, Bruskotter et al. 2017). Complete experiments (i.e. studies comprised of replication, randomisation, manipulation and control) with carnivores can rarely, if ever, be executed excellently in the field. We therefore strongly encourage future researchers to adopt controlled experimental designs whenever possible, for instance by contrasting temporal overlap in a given species pair between ecologically similar sites with low and high human disturbance (e.g. Frey et al. 2020), or across a gradient of human disturbance (e.g. Lewis et al. 2015). Choosing the right factors to control, with the right species, would eliminate some of the biases that are introduced by pooling temporal data across days and sites, and could be pivotal in detecting the effects of human disturbance on activity overlap between co-occurring species.

Carnivore communities, where temporal partitioning is not negatively affected by humans, may still experience an increase in interspecific competition following human disturbance. Indeed, increases in nocturnality can affect other dimensions of niche partitioning (e.g. increased trophic competition for nocturnal prey; Smith et al. 2018). For this reason, future studies would benefit from investigating multiple dimensions of niche partitioning simultaneously (i.e. spatial, temporal and trophic), in order to understand fully how human-induced changes in carnivore activity affect interspecific competition.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Data sources and species combinations included in the analysis. Species combinations that are found with only one reference but still had at least two coefficients of temporal overlap included in the analysis (i.e. the coefficients were calculated from two or more study areas, within the same study).

Appendix S2. Coefficients of temporal overlap reported by the eight studies comparing temporal overlaps of similar species pairs between areas classified as having low or high human disturbance.

Appendix S3. Credits for photos in Fig. 2.